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STUDIES ON CURLY-TOP DISEASE OF THE SUGAR BEET

MATERIAL

BY

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STUDIES ON CURLY-TOP DISEASE OF THE SUGAR BEET [1]

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INTRODUCTION

Curly-top [2] of sugar beets presumably was widespread before it was recognized as a distinct disease. It appears to have been confused at first with other diseases or other types of injury. The extensive losses in California, in 1899, referred to as the "California beet disease," "Western blight," etc., led to its being recognized as a distinct and serious disease, and the following year a similar condition was determined as occurring in all of the Western States where sugar beets were grown.

Linhart (*9*) [3] summarized the reports of several specialists with reference especially to California conditions. This report recorded the conditions of the areas infected but did not establish the cause or exact character of the injury.

Townsend (*19*) described and figured curly-top.

Ball (*1*) in the Annual Report for 1905 of the Utah Station announced the discovery of a causal relation between the feeding of the beet leafhopper and "curly-leaf" or "blight."

Smith (*14*) reported the severe outbreak of 1905 in California, stating that the injury was apparently physiological in character and possibly of the same general type of disease as tobacco mosaic.

Ball (*2*) emphasized, by further observation, the fact that "curly-leaf" is the result of leafhopper attack. He suggested that the disease itself might be in the nature of gall formation.

Wilhelmi (*21*) reported alkali injury as a possible cause of curly-top.

Townsend (*20*) described curly-top from both the pathological and geographical standpoints; while reaching the conclusion that the disease was a distinct systemic disease, he concluded that as yet no satisfactory explanation of the cause had been found.

Ball (*3*) adopted the name "curly-leaf" for the disease, reviewed the earlier work, and reported in considerable detail the relation of the sugar beet leafhopper and other leafhoppers to this and other injuries to the host plants. He emphasized especially that the curly-leaf condition, though produced by the leafhopper, is not due to mechanical injury by the insect nor to loss of sap. He pointed out that, in the case of injury produced in plants by related species of leafhoppers, the injury was apparently local in character; while in the case of the curly-leaf, the abnormal condition apparently spread from leaf to leaf, infecting the whole plant even though the leafhopper might have disappeared in the meantime. He also reported that the agency that caused curly-leaf was capable of remaining in the beet over winter, again producing the typical curly-leaf symptoms in the first leaves in the spring. He referred to the experimental production of "curly-leaf" in cages arranged jointly by himself and Prof. E. G.

[1] Received for publication Jan. 23, 1924.

[2] The name "curly-top" has been used in earlier publications of this Department The question of the advisability of employing "curly-leaf" instead of "curly-top" as the common name of this disease has been referred to the American Phytopathological Society.

[3] Reference is made by number (italic) to "Literature cited," p. 318-319.

Titus, by H. B. Shaw and by the Office of Sugar-Beet Investigations, Bureau of Plant Industry, United States Department of Agriculture.

Shaw (*13*) confirmed Ball's findings regarding the occurrence of curly-top in sugar beets as a result of infestation by beet leafhoppers. He caged aphids, red spiders, thrips and beet leafhoppers on sugar beets and found that curly-top developed only in the beets on which the beet leafhoppers were caged. Shaw also reported that, even though no symptoms of the disease were visible when the beets were harvested the preceding fall, curly-top disease developed during the second season in beets planted for seed production, and that the symptoms of the disease were to be found primarily upon the young or growing leaves.

Bunzel (*7*) reported a high oxidase content in the tissues of diseased beets, recalling the high oxidase content reported in earlier experiments on tobacco mosaic.

Smith and Boncquet (*16*) reported that exposure of beets for five minutes to infestation by leafhoppers was sufficient to cause the symptoms of curly-top to develop, although two weeks or more might be necessary before the symptom would be obvious. They reported a bacillus as associated with the disease.

Boncquet and Hartung (*5*) reported beet leafhoppers not necessarily able to cause the disease while, if such leafhoppers were first fed on diseased beets and then allowed to feed on healthy beets curly-top would then develop.

Smith and Boncquet (*15*) reported the finding of bacteria in the diseased beets and confirmed the report of Boncquet and Hartung of the apparent inability of the leafhopper to transmit curly-top unless it had previously fed upon diseased plants.

Ball (*4*) urged the use of the name "curly-leaf" to clearly distinguish between the disease associated with leafhopper attack and any disease having symptoms in any way similar. He reviewed the status of curly-top or "curly-leaf," especially emphasizing the geographical relation of the breeding areas of the beet leafhopper to the areas in which severe outbreaks had occurred. He also emphasized the periodicity of migrations from breeding areas and suggested the probability that epidemics of curly-leaf could be predicted through the recognition of the periodicity of the flights of the insect. Commenting on the finding by Boncquet and Hartung that the insects were apparently unable to carry the disease unless they were fed upon diseased plants, he suggested the probability that some wild plant was acting as carrier of the disease.

Boncquet and Stahl (*6*) reported the occurrence of the curly-top infection in native vegetation.

Stahl and Carsner (*17*) reported that recently emerged beet leafhoppers, lifted from the plant before feeding were not carriers of curly-top, but became carriers of the disease when fed on diseased beets.

Severin (*10*) stated that the insects caught on wild vegetation produced the disease in beets in some cases while in other cases they did not. He listed wild plants from which the leafhoppers were reared and from which these insects transmitted curly-top to sugar beets.

Carsner (*8*) reported fourteen species of plants representing eight families as susceptible to curly-top.

Severin (*11*) demonstrated that after a nonviruliferous insect has fed on a diseased plant an incubation period for at least a few hours must elapse before this insect can transmit the virus.

Stahl and Carsner (*18*) reported that when an insect is once infected the infection is apparently permanent.

The appearance of sugar beets affected with curly-top in the different stages of the disease might well be more adequately described, but for the purpose of this paper brief mention of some of the conspicuous symptoms will suffice. When a plant is infected the mature leaves remain normal in appearance, the vein swellings and curling of the leaves appearing on only the new growth. There is no conspicuous color change in the early stages of the disease (Pl. 1). In the later stages the older leaves which were mature at the time of infection

turn yellow and die, while the younger central leaves which are dwarfed and usually show conspicuous vein swellings on the under sides remain green (Pl. 2, D). The vein swellings vary with different individual plants from cases where practically every veinlet is irregularly swollen (Pl. 2, B), to cases which show only scattered, inconspicuous, rounded swellings (Pl. 2, A). The disease is characterized by a necrosis of the phloem throughout the vascular system (Pl. 3, B), and in the advanced stages of the disease this necrosis shows in the roots as dark concentric rings (Pl. 4). The exudation of a clear, viscous liquid is often conspicuous on the oldest leaves which show the vein swellings (Pl. 2, C).[4]

DISTRIBUTION OF CURLY-TOP AND THE BEET LEAFHOPPER

The geographical distribution of the curly-top disease is limited to the arid or semiarid regions of the western part of North America in which the insect *Eutettix tenella* Baker is found and to the districts adjacent to these regions. In general it may be said, therefore, that the disease occurs wherever this leafhopper is found. It has been authoritatively reported from the following States: Arizona, California, Colorado, Idaho, Kansas, Nebraska, New Mexico, Oregon, Texas, Utah, and Washington.

The disease has been reported from practically every region in California in which beets are grown. The distribution of the beet leafhopper has been studied more extensively than has the distribution of the disease, and because of its significance from the standpoint of where the disease occurs or would occur if beets were planted the localities from which the insect has been reported are listed here.

LOCALITIES FROM WHICH THE BEET LEAFHOPPER HAS BEEN REPORTED

CALIFORNIA

1. Agatha.
2. Allensworth.
3. Alpaugh.
4. Altamont Pass.
5. Alvarado.
6. Angiola.
7. Antelope Valley.
8. Arlington.
9. Bakersfield.
10. Barstow.
11. Betteravia.
12. Bitterwater.
13. Blanco.
14. Brawley.
15. Buena Vista.
16. Buttonwillow.
17. Calexico.
18. Calipatria.
19. Castaic.
20. Castroville.
21. Centerville.
22. Chino.
23. Cholame.
24. Chowchilla.
25. Chualar.
26. Claremont.
27. Coalinga.
28. Compton.
29. Connor.
30. Corcoran.
31. Coyote Wells.
32. Crows Landing.
33. Davis.
34. Dixieland.
35. Dominguez Junction.
36. Dos Palos.
37. Earlimart.
38. El Centro.
39. Famoso.
40. Gonzales.
41. Goshen Junction.
42. Hamilton City.
43. Heber.
44. Helm.
45. Hemet.
46. Holtville.
47. Huntington Beach.
48. Huron.
49. Imperial.
50. King City.
51. Lancaster.
52. Le Grand.
53. Los Alamitos.
54. Los Baños.
55. Lost Hills.
56. McKittrick.
57. Manteca.
58. Marysville.
59. Mendota.
60. Merced.
61. Milpitas.
62. Modesto.
63. Mojave River.
64. Moro Cojo.
65. Mountain View.
66. Neenach.
67. Niland.
68. Norwalk.
69. Oro Loma.
70. Oxnard.
71. Pacheco Pass (entrance).
72. Paso Robles.
73. Pleasanton.
74. Prado.
75. Ravendale.
76. Red Bluff.
77. Riverside.
78. Rosamond.
79. San Ardo.
80. San Bernardino.
81. San Fernando Valley.
82. San Jacinto.
83. San Jose.
84. San Lorenzo Creek.
85. Santa Ana.
86. Santa Margarita.
87. Sargent.
88. Saugus.
89. Shafter.
90. Soledad.
91. Spence.
92. Spreckels.
93. Stockton.
94. Tejon Pass.
95. Tracy.
96. Victorville.
97. Visalia.
98. Volta.
99. Wasco.
100. Watts.
101. Westmoreland.
102. Williams.
103. Willowbrook.

[4] The progress of the work has been greatly aided by the use of the laboratory and field facilities of the Citrus Experiment Station of the University of California. The writers are indebted to the director and the staff for many courtesies and accommodations.

OREGON

1. Echo.
2. La Grande.
3. Pendleton.
4. Union.

WASHINGTON

1. Ellensburg.
2. Granger.
3. North Yakima.
4. Pasco.
5. Sunnyside.
6. Toppenish.
7. Wenatchee.

IDAHO

1. Blackfoot.
2. Buhl.
3. Burley.
4. Gooding.
5. Hansen.
6. Idaho Falls.
7. Jerome.
8. Nampa.
9. Oakley.
10. Payette.
11. Rupert.
12. Shelley.
13. Twin Falls.

NEVADA

1. Fallon.

UTAH

1. Austin.
2. Box Elder County.
3. Delta.
4. Elsinore.
5. Fillmore.
6. Garland.
7. Lehi.
8. Lynndyl.
9. Mills.
10. Monroe.
11. Moroni.
12. Nephi.
13. Ogden.
14. Panguitch.
15. Richfield.
16. St. George.
17. St. Joseph.
18. Salina.
19. Sigurd.
20. Spanish Fork.
21. Thompsons.

ARIZONA

1. Glendale.
2. Prescott.

COLORADO

1. Fort Collins.
2. Lamar.
3. Grand Junction.
4. Rocky Ford.

NEBRASKA

1. Grand Island.

TEXAS

1. Amarillo.
2. El Paso.

NEW MEXICO

1. Las Cruces.

The localities listed include those recorded by Ball (*1*), (*4*) and Severin (*11*) and unpublished reports by W. J. Hartung, G. T. Scott, and the present writers.

ECONOMIC IMPORTANCE OF CURLY-TOP

The studies on curly-top by the writers have been conducted in the main in California, and so the consideration of the economic importance here given is based principally on California conditions. The fact should be borne in mind, however, that the disease frequently causes serious losses in the beet-growing regions of other Western States. In the regions where beets have been grown in California the losses may in general be said to have varied (within limits) directly with the distance from the coast. In cooler coastal regions or so-called fog belts the damage is usually slight or relatively unimportant. As one goes inland into the progressively warmer and more arid districts the damage caused by the disease increases so that nearly every year the resulting losses are serious and in the so-called "bad years" the losses vary from very serious to total. The losses have been so serious in some of the interior districts that vast available areas otherwise suitable for beet growing have been completely abandoned after several years of unsuccessful efforts to grow beets on an extensive commercial scale. Curly-top was, of course, not the only difficulty encountered in these hot, dry districts, but, in the opinion of the writers, it was the limiting factor.

A more definite conception of the extent of the losses which the disease has caused may be formed from Table I. These figures were kindly furnished by sugar companies operating in California. They apply to districts which the writers have had under observation. The losses, therefore, are known to be due principally to curly-top. The yield per acre for these districts in years when curly-top has not been serious has ranged from 10 to 15 tons. The losses caused by the disease may be represented graphically by showing the net yield of beets, n tons per acre, in the four localities for each of the years considered (fig. 1).

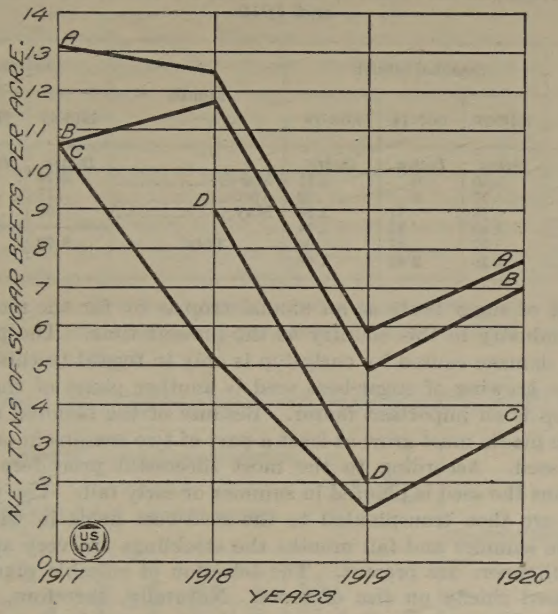

FIG. 1.—Graph showing the relative losses caused by curly-top disease

TABLE I.—*Losses caused by curly-top in four localities in California*

Locality and year	Crop area (acres)		Gross yield (tons)		Tare		Net yield per acre (tons)	Yield of sugar	
	Planted	Harvested	Harvested	Per acre	Per cent	Tons per acre		Per cent	Calculated tons per acre
District A:									
1917	1,307	1,287	17,774	13.8	5.0	0.7	13.1	19.3	2.5
1918	915	915	13,216	14.4	13.2	1.9	12.5	17.7	2.2
1919	1,288	1,288	8,349	6.5	8.2	.5	5.9	19.8	1.2
1920	933	933	7,882	8.4	8.2	.7	7.8	19.7	1.5
District B:									
1917	320	320	3,576	11.2	5	.6	10.6	19.4	2.1
1918	400	400	5,231	13.1	10.5	1.4	11.7	16.8	2
1919	675	675	3,748	5.6	8.13	.5	5.1	19	1
1920	490	470	3,601	7.7	8.4	.4	7.2	18.7	1.4
District C:									
1917	3,293	3,291	37,149	11.3	5.8	.6	10.6	19.2	2
1918	3,145	2,930	17,970	6.1	15.26	.9	5.2	16.8	.9
1919	3,425	2,550	3,664	1.4	9.18	.1	1.3	19.3	.3
1920	3,042	2,939	11,220	3.8	7.6	.3	3.5	19.8	.7
District D:									
1918	1,136	1,136	10,535.18	9.3	2.9	.3	9	17	1.5
1919	786	786	1,711.13	2.1	7.6	.2	2	17.1	.3

The question might be raised as to the possibility of other factors, such as variation in rainfall, having entered in to cause the great differences in yield. In answer to this question it may be said that irrigation is practiced in all the districts and that the amount of rainfall is therefore probably of no great significance. The rainfall is given, however, for a representative locality in the region of each of the districts A, B, and C to show the amount and distribution of the rainfall in the seasons of 1917, 1918, and 1919 (Table II).

TABLE II.—*Rainfall in the region of districts A, B, and C, seasons of 1917, 1918, and 1919*

Month	Seasonal rainfall			Month	Seasonal rainfall		
	1916–17	1917–18	1918–19		1916–17	1917–18	1918–19
	Inches	*Inches*	*Inches*		*Inches*	*Inches*	*Inches*
September	1.50	0	5.17	March	0.76	2.90	1.94
October	.37	0	.32	April	.15	.38	.08
November	.55	.71	2.39	May	.06	.09	0
December	2.40	.31	1.74				
January	.97	.47	.96	Total	8.92	7.31	15.66
February	2.16	2.45	3.06				

The growing of sugar beets as an annual crop is by far the more important phase of the industry in this country at the present time. The preceding discussion of the damage caused by curly-top is only in regard to this phase of the industry. The growing of sugar-beet seed is another phase of the industry in which curly-top is an important factor. Because of the biennial nature of the sugar beet, the plants must grow at least a part of two seasons in order to flower and produce seed. According to the most successful procedure under California conditions the seed is planted in summer or early fall. The young plants, or stecklings, are then transplanted to the seed-beet fields in winter or early spring. In the summer and fall months the stecklings are very apt to become infected if leafhoppers are present. The selection of suitable plants for transplanting is based chiefly on size of roots. Naturally, therefore, many plants which are infected late are on that account about normal in size and are transplanted to the seed fields. The result of this procedure is that a considerable proportion of the transplanted plants fail to produce flower stalks or produce only dwarfed, diseased stalks. An example of the part the disease plays was observed in the seasons of 1918 and 1919. The seed was planted late in the summer of the first year in a region infested with beet leafhoppers. As the stecklings grew up in the late summer and fall it was evident from the number of leafhoppers present and the cases of the disease scattered through the field that a considerable proportion of the plants had been inoculated. The stecklings were transplanted in the following winter and early spring with the result that because of curly-top about 30 per cent of the plants failed to produce seed.

No appreciable injury of seed beets due to infection in the second season of growth has been noted. When healthy stecklings are planted in the winter or early spring they grow to such an extent during the cool months before the leafhoppers appear or become abundant that there is practically no danger of injury from the disease. This observation is based on conditions in California, but it probably holds true also for other districts where seed beets are grown.

In addition to the direct loss due to the damage to the beet crops, great financial loss is involved when sugar factories are built in districts which prove unsuitable. The cost of building and later dismantling and removing the factory to another locality, together with the loss of capital invested in other improvements and equipment, must also be considered. Two instances in California alone are known in which factories were dismantled and removed because of the inability to grow beets on account of curly-top.

EFFECT OF CURLY-TOP ON GROWTH

A plant that becomes infected while young—when the root is perhaps 1 cm. or less in diameter—will usually die in a relatively short while or before the summer is past, but a plant that is about half grown or larger when infected will usually live a long time, as a rule to the end of the season.

Measurements made during two seasons of the roots of beets affected with curly-top show that increase in size of the root usually continues for a considerable length of time, often more than a month after the plant has become evidently diseased. The data taken during one season are listed in Table III. The plants were grown at Riverside, Calif. Figures are given of the size and number of the leaves of each plant, because the vigor of growth of the root is correlated with the size of the top. Plants which were evidently diseased on May 14 continued to grow, so that by July 26 the roots of most of them had nearly doubled in diameter. The measurements in connection with observations of the affected plants indicate that increase in size of roots continues as long as the older leaves, which were mature at the time of infection and therefore have remained apparently normal, survive. The weight of the top or leaves, as well as that of the root of each plant at the time of digging on July 26, is given. These figures indicate the great retarding effect of the disease on the growth of the tops. It is of interest to note the wide variations in individual plants as to the effect of the disease. The variation appears to be greater than that which occurs in the case of diseases of many plants.

TABLE III.—*Effect of curly-top on the growth of sugar beets*

Plant	Maximum leaf and root dimensions							Weight on July 26		Date of observation and degree of disease when first noted
	Leaves on May 14		Root diameters							
	Number of leaves on May 14	Width	Spread	On May 14	On June 2	Increase in 19 days	On July 26	Increase in 54 days	Top	Root	
		Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Gm.*	*Gm.*	
No. 3	10	10.2	43	2.09	3.57	1.48	3.98	0.41	27	78	May 14, two leaves affected.
No. 6	18	13.3	56	3.62	5.53	1.91	6.49	.96	62	207	May 14, five youngest leaves affected.
No. 8	16	11.4	52	3.38	5.51	2.13	5.71	.20	49.5	169	May 14, one leaf affected.
No. 12	15	15.9	53	3.10	4.98	1.88	5.85	.87	89.5	272	May 14, three youngest leaves affected.
No. 19	17	16.5	64	3.02	4.63	1.61	5.84	1.21	87	185	May 14, seven youngest leaves affected.
No. 20	15	12.7	62	3.80	5.02	1.22	5.20	.18	43.5	120	May 14, six of younger leaves affected.
No. 22	18	15	56	3.79	6.35	2.56	7.88	1.53	147	385	May 14, seven of younger leaves affected.
No. 32	15	13.3	62	2.98	4.50	1.52	5.26	.76	26	125	May 14, three of younger leaves affected.
No. 35	21	10.8	76	3.90	5.32	1.42	5.54	.22	74.5	114	May 14, nine of younger leaves affected.
No. 36	19	20.3	70	4.10	5.97	1.87	5.71	−.26	22.5	186	May 14, four of younger leaves affected.
No. 38	12	10.8	63	2.41	3.08	.67	2.88	−.20	10	20.5	May 14, five of younger leaves affected.
No. 2	14	10.2	46	2.35	4.70	2.35	7.12	2.42	132	276	June 2, one young leaf affected.
No. 4	8	6.4	47	1.19	3.02	1.83	4.54	1.52	55	112	June 2, four of younger leaves affected.
No. 5	15	17.8	51	2.77	5.56	2.79	7.63	2.07	153	417	June 2, eight youngest leaves affected.
No. 10	10	8.3	58	1.23	3.10	1.87	3.60	.50	22	48.5	June 2, six youngest leaves affected.
No. 11	19	15.9	61	4.62	7.49	2.87	8.06	.57	90	440	June 2, four youngest leaves affected.
No. 13	11	14	53	3.25	5.78	2.53	6.94	1.16	175	380	Do.
No. 14	10	15	66	3.03	5.60	2.57	7.67	2.07	300	440	June 2, five of younger leaves affected.

TABLE III.—*Effect of curly-top on the growth of sugar beets*—Continued

Plant	Number of leaves on May 14	Maximum leaf and root dimensions							Weight on July 26 (grams)		Date of observation and degree of disease when first noted
		Leaves on May 14		Root diameters							
		Width	Spread	On May 14	On June 2	Increase in 19 days	On July 26	Increase in 54 days	Top	Root	
		Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Gm.*	*Gm.*	
No. 16	24	12.7	66	3.99	7.28	3.29	7.61	0.33	52	252	June 2.
No. 23	12	14.6	60	2.72	5.25	2.53	6.70	1.45	83	207	June 2, two youngest leaves affected.
No. 26	20	17.8	61	4.69	8.69	4.00	10.82	2.13	185	753.5	June 2.
No. 27	19	14	69	3.89	6.76	2.87	8.72	1.96	152.5	449	June 2, three of younger leaves affected.
No. 28	16	20	74	3.61	6.40	2.79	8.20	1.80	169	300	June 2, seven of younger leaves affected.
No. 31	15	16.5	81	4.15	6.99	2.84	8.13	1.14	19	425	June 2, about half of the leaves affected.
No. 37	9	8.3	55	1.60	3.36	1.76	4.32	.96	22	64	June 2, one young leaf affected.
No. 9	16	16.5	69	3.93	7.90	3.97	10.23	2.33	321	802	June 2, healthy.
No. 15	12	14.6	77	2.69	5.25	2.57	6.71	1.46	68	300	Do.
No. 17	13	21.6	79	5.83	9.76	3.93	10.95	1.19	301.5	896.5	Do.
No. 24	13	10.2	53	2.18	4.79	2.61	8.24	3.45	225	438	Do.
No. 30	13	10.2	48	3.11	5.22	2.11	6.46	1.24	116	306.5	Do.

DRY WEIGHT OF TOPS INCREASED

Moisture determinations which were made at three different times of the tops or leaves of young healthy and diseased beets show that the proportion of dry weight of the tops of young diseased plants exceeds the proportion of dry weight of those of young healthy plants by 2.5 to 3 per cent. This excess of dry weight is attributed to the excessive accumulation of carbohydrates, probably sugars. Due to the breaking down of the phloem, normal translocation is impossible. The clear, viscous exudate (Pl. 2, C) has been repeatedly found by Fehling's test after hydrolysis with an acid to contain a complex sugar, probably saccharose. In only one or two instances were traces of reducing sugars detected. The escape of the exudate by rupturing the tissue is attributed to the high pressure developed by the abnormal accumulation of the sugars.

TABLE IV.—*Artificial inoculations of sugar beets, resulting in no disease* [a]

Date	Kind of inoculum	Kind and number of plants inoculated	Method of inoculation
Season of 1918:			
March 3	Fresh excreta of the leaf hopper.	Two young beet seedlings.	Point of steel needle dipped into drops of excreta and then pricked into plants.
August 3	Ringer's solution extract and aqueous extract of young leaf of curly-top beet.	Four young beet seedlings.	Sprayed each extract on two plants; then caged on each five nonviruliferous leafhoppers.
August 12	Six adult leafhoppers macerated in 2 cc. of Ringer's solution.	Three young beets.	A drop of inoculum placed on each of two leaves of each plant and pricked in with small steel needles.
Do	Curly-top beet leaf macerated in Ringer's solution.	----do----	Do.
Do	Curly-top beet leaf macerated in distilled water.	----do----	Do.
Season of 1919:			
May 24	Pieces of curly-top beet leaf	Eight beets (these had five or six true leaves).	Placed tissue on midrib near base of blade, macerating over and pressing into a slit in the midrib.
August 8	Pieces of petiole of leaf of curly-top beet.	Seven young beets.	Placed tissue on center of blade of one leaf of each and then macerated into wound in the blade with scalpel and needle.

[a] Since this manuscript was prepared curly-top has been artificially communicated by transferring juice from diseased to healthy beets, as described in the following publications: SEVERIN, H. P. CURLY LEAF TRANSMISSION EXPERIMENTS. Phytopathology 14: 80–93, illus. 1924: CARSNER, E., and STAHL, C. F. PROGRESS REPORT ON CURLY-TOP OF THE SUGAR BEET. (Abstract) Phytopathology 14: 122–123. 1924.

TABLE IV.—*Artificial inoculations of sugar beets, resulting in no disease*—Contd.

Date	Kind of inoculum	Kind and number of plants inoculated	Method of inoculation
Season of 1919—Continued.			
August 8	Entire viruliferous leafhopper.	Seven young beets.	One insect macerated on and pricked into a leaf of each plant. Insect first stunned by a gentle pressure between the fingers.
August 13	Two entire curly-top plants macerated in distilled water.	Three young beets.	About 500 cc. of the extract poured on the soil around the roots.
Do	Part of the preceding extract	Several young plants.	Plants dug with as little injury to the roots as possible and roots placed in extract for one hour; older leaves then removed and plants replanted.
August 27	Distilled-water extract of two entire curly-top beets.	Several beet plants with roots one-fourth inch in diameter.	Roots placed in the extract for one hour; older leaves then removed and plants replanted.
October 2	Pieces of midrib of badly affected leaf of a curly-top beet.	One young beet	Tissue placed in a slit in the petiole; wound not covered.
Do	Piece of midrib of curly-top beet leaf.	One beet seedling	Tissue placed in a slit in the hypocotyl; wound covered with soil.
Do	A leafhopper nymph from a curly-top beet.	One young beet	Insect forced into a slit in the petiole of the plant; wound bound with cloth and grafting wax.
Do	Adult leafhopper from a curly-top plant.	One beet seedling	Insect pressed into a slit in the hypocotyl; wound wrapped and covered with grafting wax.
Do	Entire viruliferous insect	Three beet plants with ½-inch roots.	One insect in a slit in the crown of each plant just below the ground level.
October 18	Small piece of petiole of a leaf of a curly-top beet.	Three young beets	Tissues placed in a slit in the root just below ground level; wound covered with soil.
October 21	Tops and roots of curly-top beets separately extracted in distilled water.	Eight plants with ½-inch roots.	Roots allowed to stand in extract over night; leaves then removed and roots replanted.
Season of 1920:			
April 27	Extract of entire curly-top plant in distilled water.	Several beets	Healthy leaves cut and cut ends placed in vials of the extract; nonviruliferous leafhoppers placed on these for two days and then on healthy beets.
May 2	Tap-water extract of two entire young curly-top beets which had been macerated in a mortar.	Three young beet plants	Slowly injected through fine glass nozzles attached to a funnel containing the extract, which was so elevated as to cause a gentle pressure of the liquid.
May 12	Tap-water extract of two entire curly-top beets which had been macerated in a mortar.	Two young beet plants.	Cut ends of petioles of healthy leaves placed in vials of the extract; seven nonviruliferous insects were then caged on the blades of these leaves for three days and then transferred to healthy plants.
May 15	Expressed juice of 12 young curly-top beets.	Several young beets.	Plants dug and roots allowed to stand in the juice for four hours and then replanted.
Do	Expressed juice of curly-top plants and expressed juice diluted with equal parts of tap water.	——do——	Roots placed in the two solutions for four hours and then replanted.
Do	——do——	——do——	Cut ends of petioles of healthy leaves placed in vials of the extract and nonviruliferous insects placed on them for four days and then transferred to healthy beets.
July 5	Parts of viruliferous leafhoppers which had been anæsthetized with ether to facilitate dissection.	Twenty-one young beets.	Parts of insects (e. g., heads, thorax, and abdomen) were placed in Ringer's solution, then on each plant an insect part was inoculated into the base of the blade of each of the first true leaves by means of a sharp steel needle.
Season of 1921:			
May 3	Juice of a curly-top plant extracted by means of a hypodermic syringe.	Seven beet plants. One had only cotyledons; the others had seven leaves.	Juice slowly injected by means of hypodermic syringe immediately after it was extracted from diseased plant. Injected into crowns and cut end of a petiole.

TABLE V.—*Inoculation of sugar beets with insects other than Eutettix tenella, no disease resulting*

Season, number, and date	Species of insect	Number of insects used	Length of time insects were on curly-top beets	Healthy plant to which the insects were transferred	Length of time insects were left on healthy plants
Season of 1915:					
No. 1, Aug. 30	Empoasca viridescens	5	4 days	Young beet	28 days.
No. 2, Aug. 30	Agallia spp	2	do	do	Do.
No. 3, Aug. 30	Thamnotettix geminatus (?).	1	do	do	Do.
No. 4, Aug. 30	Cicadula 6-notata	2	do	do	Do.
No. 5, Aug. 30	Liburna sp	1	do	do	Do.
No. 6, (?)	Empoasca viridescens	(?)	Collected from diseased plants.	do	22 days.
No. 7, (?)	Agallia spp	(?)	Collected from diseased plants in the field.	do	Do.
Season of 1917:					
No. 8, Aug. 29	Empoasca viridescens	7	47 days	(a)	47 days.
No. 9, Aug. 29	Agallia cinerea	7	35 days	(a)	35 days.
No. 10, Sept. 4	Empoasca viridescens	6	39 days	(a)	39 days.
No. 11, Sept. 4	Nysius sp	6	29 days	(a)	29 days.
No. 12, Sept. 4	White fly (Aleyrodidae)	12	do	(a)	Do.
Season of 1917:					
No. 13, Sept. 14	Aphis sp	Large.		(2) (b)	
No. 14, Sept. 14	do	Large.		(3) (c)	
No. 15, Sept. 4	Lygus pratensis	10	29 days	(a)	29 days.
Season of 1919:					
No. 16, May 22	Acinopterus sp	3	4 days	Young beet	15 days.
No. 17, May 22	Chlorotettix sp	3	do	do	Do.
No. 18, May 22	Agallia sp. (large)	(?)	do	do	Do.
No. 19, May 22	Agallia cinerea	3	13 days	do	44 days.
No. 20, May 22	Empoasca viridescens	5	20 days	do	37 days.
No. 21, July 1	Thamnotettix montanus	4	4 days	do	27 days.
No. 22, (?)	Aphis sp	Large.	3 days	(d)	
No. 23, Apr. 28	Eutettix strobi	3	2 days	Young beets	2 days.
Season of 1920:					
No. 24, Feb. 23	Empoasca viridescens	6	Several days	Young beets and *Stellaria media*.	18 days.

[a] The insects were placed in a cage with a small curly-top beet and a small healthy beet for the number of days stated.

[b] A curly-top beet leaf heavily infested with aphids was placed in a cage with healthy and curly-top plants. The insects colonized on both plants.

[c] A curly-top beet leaf heavily infested with aphids was placed in a cage with a healthy plant upon which the insects colonized.

[d] A curly-top leaf with aphids on it was removed to a cage with a healthy beet and another to a cage with two healthy *Stellaria media* plants.

Observational evidence agrees with these negative results from attempts to transmit the disease by insects in so far as aphids and *Empoasca viridescens* are concerned. These two species have been repeatedly observed infesting the plants in cages which contained both curly-top and healthy plants and in no case has there been any evidence that they transmitted the virus of the disease.

The question of transmission by grafting perhaps should be considered in this connection. Smith and Boncquet (*15*) claim to have transmitted the disease by grafting parts of diseased beets on to healthy plants. Thus far the present writers have been unable to successfully graft parts of a curly-top plant on to a healthy plant, and the attempts to make these grafts have not produced the disease.

IS THERE AN INCUBATION PERIOD IN THE LEAFHOPPER?

As has previously been stated, *Eutettix tenella* is the only known agent or means by which the virus of curly-top can be transmitted. Also, the fact has been pointed out that the ability to produce the disease is not an inherent characteristic

of the insect. In view of these facts the question as to whether or not an appreciable interval of time must elapse after a nonviruliferous [5] leafhopper has fed on a diseased plant before it is able to effectively transmit the virus may have some significance regarding the nature of the virus. Smith and Boncquet (*15*) state that a period of at least 24 hours but not more than 48 hours must elapse. Severin (*11*) worked with batches of 25 to 50 insects instead of single leafhoppers. He found that at high temperatures (about 100° F.) the insects were occasionally able to produce the disease within four to six hours after they had been placed on a diseased plant. For this short period his results showed 8 cases of disease from 60 tests. No positive results were obtained from 36 tests for a period of one to three hours. Periods of 24 to 48 hours after the insects were placed on the diseased plant gave a greater proportion of positve results than shorter ones. The experimental tests which the writers have thus far made in regard to this question are listed in Table VI. In each of these experiments nonviruliferous leafhoppers were placed on a curly-top beet for a given number of hours and then transferred individually to young healthy plants for a certain number of hours and then transferred again, etc. For example, in experiment No. 1 the nonviruliferous insects were caged on a curly-top plant for 24 hours and then caged singly on healthy plants for the same length of time. The first period tested was from 24 to 48 hours after the insects were placed on the diseased plant. After that the insects or those which still survived were transferred to other healthy plants for 24 hours. This second period, therefore, was from 48 to 72 hours after the insects were placed on the diseased plant. The successive transfers of the same insects are indicated in Table VI by attaching the letters *a*, *b*, *c*, etc., to the number of the experiment.

The results show that some of the insects were able to transmit the virus within a period of 21 hours and 45 minutes after they were placed on the diseased beet. In another case the period was 22 hours and 20 minutes, and in a third case it was 23 hours. In some cases the insects all failed to produce the disease within periods of 24 hours or less. A point which may be of some significance is that the results seem to indicate that a greater number of the insects become able to transmit the virus after a longer period than 24 hours than are able to do so in the shorter time. The facts cited seem to indicate that a multiplication of the causal agent takes place within the insect.

RELATION OF THE NUMBER OF INSECTS TO CURLY-TOP

Comparative inoculations were made at the same time and on similar plants with different numbers of insects. The object was to determine whether or not the quantity of virus injected was significant in producing the disease or in regard to the period of incubation. Twelve experiments have been performed to test this. The procedure in these tests was so varied that the details can not be readily tabulated. The results, however, may be summarized. They indicate that when 10 insects are used the inoculated plant is more likely to become diseased than when the inoculation is made with 1 or 2 insects. It seems probable that this fact is due to the variation of individual insects in regard to infection rather than to the quantity of virus injected. In the cases where the disease is produced there is no difference in the incubation period or severity of the effect between inoculations with single insects and those with 10 insects.

[5] It has recently been brought to the writers' attention that the term *viruliferous* occurs in medical literature; and as it appears to have the same meaning as viriferous (meaning virus-bearing) used by the writers in previous publications, it is of course desirable to use *viruliferous* for the sake of preventing a duplication of terms.

TABLE VI.—*Length of incubation period in the leafhopper before becoming viruliferous*

Date started	Experiment No.	Length of time			Number of insects		Remarks
		On curly-top plant	On healthy plants	Total	Tested	Producing the disease	
Season of, 1918:		*Hours*	*Hours*	*Hours*			
July 17	1*a*	24	24	48	20	1	Inoculated plants in 5-inch pots.
Do	1*b*	----	24	72	14	5	Plants in bed in green-house. More favorable conditions for growth may have been a factor.
Do	2*a*	24	24	48	20	5	
Do	2*b*	----	24	72	20	9	One insect which produced the disease in the first period failed to do so in the second period, so that five more than in the first period were then effectively viruliferous.
August 14	3*a*	24	24	48	30	5	
Do	3*b*	----	24	72	30	6	
September 2	4*a*	----	24	48	30	10	*Stellaria media* plants were used instead of beets.
Do	4*b*	----	24	72	28	22	One insect which caused disease in the first period did not cause it in the second, so there was in the second period an increase of 13 that were effectively viruliferous.
Do	4*c*	----	24	96	26	15	
November 8	5*a*	5	18	23	26	11	*Stellaria media* plants were used instead of beets.
Do	5*b*	----	73	96	24	22	The second period was so much longer than the first that a fair basis of comparison is hardly afforded.
Season of 1920:							
August 23	6*a*	3	19½	22½	5	----	
Do	6*b*	----	9	31½	5	----	
Do	6*c*	----	15	46½	5	1	
Do	6*d*	----	72	120	5	1	
Do	7*a*	7	15½	22½	4	1	
Do	7*b*	----	9½	31½	4	3	
Do	7*c*	----	15	46½	4	----	
Do	7*d*	----	72	120	4	2	One of the four insects did not produce the disease at all.
September 13	8*a*	5¾	17	22¾	10	----	
Do	8*b*	----	7½	30	10	1	Insect No. 8 produced the disease.
Do	8*c*	----	17¼	47½	10	3	Nos. 5, 7, and 10, produced the disease.
Do	8*d*	----	144	192	10	4	Nos. 6, 7, 9, and 10, produced the disease; four of the insects did not produce the disease at all.
September 14	9*a*	4½	17¼	21¾	10	2	Nos. 2 and 7 produced the disease.
Do	9*b*	----	7¾	29½	10	----	
Do	9*c*	----	72	96	10	3	Nos. 2, 5, and 7 produced the disease; seven of the insects did not produce the disease at all
September 22	10*a*	6	2½	240	10	----	
Do	10*b*	----	15	23½	5	----	
Do	10*c*	----	8	31½	10	1	No. 10 produced the disease.
Do	10*d*	----	6	47½	10	2	Nos. 1 and 6 produced the disease.
Do	10*e*	----	8	55½	10	1	No. 2 produced the disease.
Do	10*f*	----	16½	72	10	----	
Do	10*g*	----	240	312	10	4	No. 1, 4, 6, and 10, produced the disease; five of the insects did not produce the disease at all.

VARIATION OF INDIVIDUAL INSECTS IN REGARD TO INFECTION

In the attempt to determine whether or not there is any uniformity of behavior among individual leafhoppers in regard to producing the disease, a considerable number of insects were caged singly on individual plants, under similar conditions, on beets or other susceptible plants for periods of 24 hours or longer on consecutive days. Tests of this nature were repeatedly made, using 3 to 30 individual insects in a test. The results of two of these tests or series are brought together in Table VII.

The question has been raised as to whether the infectivity of the insect or ability to produce the disease runs in cycles, such as might occur if the virus were an organism with a definite life cycle. The results as listed in Table VII seem to give no evidence of definite cycles of infectivity. The evidence seems to justify the conclusion that, in general, when an insect has produced or failed to produce the disease in a given period it is more likely to give a similar result in the subsequent one or more periods before changing to the other result. In other words, the positive or negative results are more likely to be grouped together in consecutive periods than they are to alternate. This idea is based on the results shown in the table, as well as on the results of other tests. As to what is the significance of this seeming tendency of the results, the evidence thus far justifies only speculation. It is of interest to note the preponderance in the number of cases in which the disease was produced over the number of negative results.

TABLE VII.—*Variation of individual insects in regard to causing infection*

[The plus sign (+) indicates the production of the disease, and the minus sign (−) indicates that no disease resulted]

Inoculation period	Insect No.																														Total for each period	
Hours	6	7	9	12	13	21	22	53	54	55	56	57	58	59	60	61	63	65	66	67	68	69	71	72	73	86	87	88	89		+	−
24	+	+	+	+	+	+	−																								6	1
384	+	+	+	+	−	+	+																								6	1
24	−	+	+	+	+	+	+																								6	1
24	+	+	+	+	+	+	+																								7	0
24	+	+	−	+	+	+	+																								5	2
24	+	+	+	+	+	+	+																								6	0
24	+	+	+	+	−	−																									4	2
24	−	−	−	−	−	−																									0	4
48	+	−	−	−	−	−																									1	4
24	−	−	+	+	−	+																									3	2
24	−	+	−	+	−	−																									2	3
24	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−		1	0
24	−	−	−	−	−	−	−	−	−	+	−	+	+	+	+	−	−	−	+	−	+	+	−	−	−	−	−	−	−		8	8
48	−	−	−	−	−	−	−	−	+	−	+	+	+	+	+	−	−	+	−	+	−	+	−	−	−	−	−	−	−		10	6
24	−	−	−	−	−	−	−	+	−	+	−	+	−	+	−	+	−	+	−	−	−	−	+	−	−	−	−	−	−		8	9
24	−	−	−	−	−	−	−	+	−	+	−	−	−	−	−	−	+	−	+	−	−	−	+	−	−	−	−	−	−		5	13
24	−	−	−	−	−	−	−	+	+	+	−	+	+	+	+	+	+	+	+	−	+	−	−	+	−	−	−	−	−		14	3
72	−	−	−	−	−	−	−	+	+	−	+	+	−	−	+	+	+	−	−	+	−	+	−	−	+	−	−	−	−		11	2
72	−	−	−	−	−	−	−	+	−	−	−	+	+	−	−	−	+	+	−	−	+	−	+	−	+	−	−	−	−		8	5
72	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	−	−	+	−	−	+	−	−	+	−	−	−	−		4	7
24	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	−	−	+	−	−	+	+	−	−	−	−		5	6
48	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	−	−	+	−	+	−	+	−	−	−	−	−	−	−		7	3
48	−	−	−	−	−	−	−	−	−	−	+	+	−	+	−	+	−	−	+	−	+	+	−	+	−	+	−	+	−		10	3
48	−	−	−	−	−	−	−	−	−	−	+	+	−	+	−	+	−	+	−	+	+	+	−	+	+	+	+	+	+		13	1
48	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	+	−	+	−	−	+	+	−	−	+	−		6	8
120	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	+	−	+	−	−	+	−	−	−	−	+	+		7	7
24	−	−	−	−	−	−	−	−	−	−	−	+	−	+	−	+	−	−	−	−	+	−	+	−	+	−	+	−	−		7	5
24	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	+	−	+	−	+	+	−	−	−	−	−		6	5
48	−	−	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	+	−	+	−	+	−	+	−	+	−	−		7	4
72	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	+	−	+	−	−	+	−	−	+	+	−		6	5
24	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−	−	−		4	7
72	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	−	−	+	−	−		3	7
168	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	−	−	−	+	−	+	−	−	−	−	−	−		4	5
24	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	+	+	−	−	−	−	−	+	+	+	−	−	+	−		8	2
216	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	−	+	−	+	−	+	−	+	−	−		7	4
24	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	+	−	+	−	+	+	−	−	−	−	−		5	2
Total for each insect:																																
Plus	8	8	7	8	5	7	4	5	3	4	2	11	12	4	15	5	12	9	1	17	5	18	2	19	8	7	1	10	3	220		
Minus	3	3	4	3	2	4	1	2	6	2	4	5	10	1	7	1	10	12	5	6	17	5	3	2	13	6	5	2	3			147

The numbers at the top of the columns were used to designate the individual insects. The figures in the left-hand column show the number of hours the insects were on the plants. The plus sign (+) indicates that the disease was produced as a result of the inoculation in that period. Likewise the minus sign (−) indicates that

curly-top was not produced in a given period. The periods represented between any two of the horizontal lines show the number of insects used on any one day or period. Where the columns are very short the fact is to be inferred that the insect concerned soon escaped or died. A blank in a column indicates that no note was obtained for that period, owing to the fact that the tag label could not be found.

RELATION OF LIGHT TO INFECTION

A limited amount of experimental work has been done in the attempt to determine whether or not light is necessary for infection to occur. Young beet plants were kept in darkness for a period and then inoculated in comparison with a series of plants exposed to daylight. In each experiment some of the plants were inoculated on the cotyledons and others on the true leaves. The details of the procedure and the results are listed in Table VIII.

TABLE VIII.—*Relation of light to infection of beet plants tested in 1920*

Experiment and date	Length of time			Point of inoculation	Number of plants inoculated	Diseased
	In the dark before inoculation	Insects on plants	In the dark			
	Hours	*Hours*	*Hours*			
No. 1, Mar. 24	48	72	120	Cotyledons	5	[a] 2
	48	72	120	First true leaves	5	[b] 1
No. 2, Apr. 1	26	22	48	Cotyledons	3	3
	26	22	48	First true leaves	3	1
No. 3, Apr. 24	34	21	55	Cotyledons	8	3
	34	21	55	First true leaves	7	1
	[c]	21	----------	Cotyledons	8	2
	[c]	21	----------	First true leaves	7	4
No. 4, Nov. 25	19	26	65	Cotyledons	6	6
	19	26	65	First true leaves	6	3
	[c]	20	----------	Cotyledons	4	4
	[c]	20	----------	First true leaves	4	4
No. 5, Dec. 4	22	20	42	Cotyledons	4	2
	22	20	42	First true leaves	4	0
	[c]	20	----------	Cotyledons	4	1
	[c]	20	----------	First true leaves	4	2

[a] Only four lived. [b] Only two lived. [c] Not placed in the dark.

In each test plants of the same age were used throughout, and they were grown under conditions as nearly similar as possible except in regard to light. If any significance may be attached to the results of these few tests, they indicate that, with young plants which have been kept in darkness for about 24 hours prior to inoculation, infection can be more readily effected on the cotyledon than on the leaves. Plants exposed to usual daylight, on the other hand, seem about as easily infected on the true leaves as on the cotyledons. If these facts be true, it would seem logical to presume that the presence of food substance as stored products in the cotyledons or from the process of photosynthesis in all green parts facilitates infection. It seems worthy of note that in test No. 1, where the plants were kept in darkness for five days, only two of the five leafhoppers caged on the true leaves survived, while all five of those on the cotyledons lived. Probably those on the true leaves were starved.

EFFECT OF HEAT ON THE VIRUS

The question as to whether or not the virus of curly-top is destroyed by relatively high temperatures was studied by placing nonviruliferous leafhoppers on parts of curly-top beets which had been immersed in water at the desired temperature. The root pieces were cut so that in no case was the thickness greater than 1 cm. A period of 10 minutes was used in each experiment. After the leaves or root pieces had been immersed in the heated water, nonviruliferous insects were caged on these beet parts for 24 hours and then removed to healthy plants. The results of the experiments are shown in Table IX. It should be noted that in the cases where the insects failed to secure the virus from heated leaves the leaves were so decomposed by heat as to be unfit for food. The results of the experiments seem to indicate that the virus is not destroyed by temperatures lower than those at which the beet tissue is killed. Many bacterial parasites of plants are killed by temperatures lower than those which the curly-top virus will endure.

TABLE IX.—*Effect of the application of heat on the virus of curly-top*

Season, experiment, and date	Temperature of water used (°C.)	Parts of diseased plant heated	Results
Season of 1919:			
Number 1, April 29	45 to 46	Leaves	Plants diseased.
Number 1, April 29	54 to 55	do	Plants healthy.
Number 2, May 8	45	Leaf	Plants diseased.
Number 2, May 8	50	do	Plants healthy.
Number 3, June 6	49 to 50	Leaves	Plants diseased.
Number 4, August 7	49.5 to 50	do	Do.
Number 4, August 7	51 to 52	do	Do.
Season of 1920:			
Number 5, April 14	51 to 52	do	Do.
Season of 1921:			
Number 6, October 14	51 to 52	Leaves and root pieces	Do.
Number 6, October 20	52 to 53	do	Do.
Number 6, October 20	60 to 61	Leaves	Plants healthy.
Number 6, October 20	60 to 61	Root pieces	Plants diseased.

EFFECT OF DESICCATION ON THE VIRUS

Four tests in which dried tissue of curly-top beets was remoistened with water and then placed in cages as food for nonviruliferous leafhoppers have given only negative results. The insects were unable to produce curly-top when removed to healthy plants. The survival of the insects in three of the tests for periods of approximately 24 hours at room temperature indicates that they must have fed to some extent on the old diseased tissue. Further work is needed to justify the conclusion that the virus is destroyed by desiccation.

DISTRIBUTION OF VIRUS IN AFFECTED PLANTS

Those leaves which are mature at the time of infection remain normal or free from symptoms of the disease until they begin to yellow with age. The question has therefore been suggested as to whether or not these apparently normal leaves contained the virus or disease-causing factor. Tests have been made by the use of nonviruliferous leafhoppers. These insects were caged on the leaves to be tested and then transferred to healthy beet plants to determine if they had become effectively viruliferous. Eight trials of this nature have been made. In a few instances the insects failed to secure the virus from the old, normal-appearing

leaves. In most of the trials, however, the insects secured the virus from the normal-appearing leaves as well as from the younger, evidently diseased leaves. The peculiar fact should be noted, however, that the insects which were placed on the leaves showing the symptoms were able to transmit the virus sooner than those insects which were placed on the older, normal-appearing leaves.

The fact that the virus is present in the roots of diseased plants has been repeatedly determined by the use of nonviruliferous insects.

IS A BACTERIAL ORGANISM ASSOCIATED WITH CURLY-TOP?

The discovery of a bacterial organism associated with beets affected by curly-top was announced by Smith and Boncquet (*15*) and earlier workers. The work of the present writers on this point may be divided into two phases. In the first place, attempts have been made to grow beet plants under aseptic conditions by the use of steamed soil and disinfected seed. The plants were covered with bell jars to protect them from contamination by air-borne organisms. After curly-top had been produced in some of the plants, pieces of affected leaves of these were transferred, without disinfection, to tubes or plates of a culture medium. Bacteria grew from the leaf pieces in some instances, but the important phase of the results is that in several of the cases the medium into which the curly-top tissue was introduced remained sterile or showed only fungus contamination.

The other phase of the study of the question has been the plating of pieces of tissue of curly-top plants. Pieces of the interior of roots and of petioles have been cut out with aseptic precautions and then plated without disinfection. Pieces of diseased leaves have been plated after disinfection with mercuric chlorid for 5 to 15 minutes. In the majority of the cases both the untreated and the disinfected tissue remained sterile. In some instances bacteria grew from the tissue pieces, but several different types were represented. None of these were tested by inoculation.

The results of these two lines of work indicate at least that no easily culturable specific bacterial organism is constantly associated with curly-top. That bacteria may get into curly-top tissues through the open wounds caused by the dying back of lateral roots and the ruptures on the leaves made by the liquid exudate seems probable.

THE INCUBATION PERIOD OF THE DISEASE

The length of time that elapses from the inoculation of the plant until the first symptoms appear is considered as the incubation period of the disease. Temperature affects the length of the period, as is noted elsewhere in this paper. The incubation period is shortest when, with high temperatures, conditions are still favorable for growth of the plant. With beet plants in cheesecloth cages out-of-doors in the summer at Riverside, Calif., as short an incubation period as four days has been occasionally noted. With *Stellaria media* an incubation period of four days has several times been observed. In one case with this plant symptoms were visible within 48 hours after inoculation. In general the incubation period in sugar beets varies from 7 to 14 days. With low temperatures or conditions otherwise unfavorable for growth the period may be prolonged, sometimes for a month or more.

The discussion of the incubation period of the disease as given here should not be confused with the discussion by Severin (*11*). He speaks of the time elapsing between inoculations and when "noninfective" insects were able to secure the causative agent from the plant as the incubation period of the causative agent.

RELATION OF TEMPERATURE TO CURLY-TOP

The writers' ideas as to the relation of temperature to the incubation and development of curly-top are based principally on observations made under natural conditions at different seasons. Facilities for accurately controlling temperatures where plants were grown in California have not been available, but the evidence obtained indicates that soil temperature as well as that of the air affects the duration of the incubation period in beets. For instance, in an experiment where all the inoculated plants were exposed to the same range of air temperatures but were exposed to two different soil temperatures, symptoms of the disease appeared first at the higher temperature. With the plants where the maximum soil temperature ranged from 25° to 35° C. symptoms of curly-top appeared on the eighth day, while in the case of the plants where the maximum temperature varied from 15° to 20.5° C. symptoms first appeared on the eleventh day. Results of two series of tests conducted with controlled soil temperatures in a greenhouse at Madison, Wis.,[6] support the view as to the influence of soil temperatures. Plants inoculated in California and sent by mail to Madison and there grown at a soil temperature of 33° C. developed the symptoms sooner than did those at 15° C. In the case of *Stellaria media* the results of one test indicate that soil temperature is less important than in the case of the beet. Where the air temperature was the same for both sets of plants the symptoms appeared at the same time in both the high and low temperature soil. If this seeming difference between beets and chickweed holds true it may possibly be explained on the basis of the different structure of the two plants. In the case of the beet the virus has to pass through the crown of the plant, which is usually at or below the soil level, in order to reach the new leaves. The main shoots of a *Stellaria media* plant throw out lateral branches, so that the curly-top virus may reach new leaves without necessarily passing through the root or crown. It would, therefore, probably be influenced in its rate of spread or development chiefly by the air temperature.

Low temperatures retard the progress of the disease as they lengthen the incubation period. This fact probably explains why curly-top is generally less injurious, even when it occurs in the cooler coastal districts, than it is in the warmer regions.

AGE OF PLANTS IN RELATION TO SUSCEPTIBILITY

The question of the relation of the age of a plant to its susceptibility to curly-top infection is of great interest from the standpoint of cultural practice as to time of planting. Field observations indicate that if beets have attained a considerable size before the leafhoppers appear they are much more likely to make a harvestable crop than they will if very small when the leafhoppers come in. This fact seems due, in part at least, to the beets becoming less easily infected as they grow older. A limited amount of experimental work on the question, which is detailed in Table X, supports this idea. In the experiments where plants of different ages were inoculated on the same date both lots were growing under similar conditions. The age of the plants used is indicated in the table by giving the number of leaves developed.

[6] The details of the tests at Madison were handled by Hurley Fellows.

TABLE X.—*Age of sugar beet plants in relation to susceptibility*

Season, experiment, and date	Age of plants	Insects per plant	Number of plants	
			Inoculated	Diseased
Season of 1920:				
No. 1, January 2	6 to 8 leaf stage	1	35	22
No. 2, March 13	Cotyledon stage	1	6	2
	6 to 7 leaf stage	1	6	0
No. 3, March 17	Cotyledons and first pair of leaves	1	6	4
	7 to 8 leaf stage	1	6	1
No. 4, March 31	Cotyledons and first pair of leaves	1	15	8
	6 to 8 leaf stage	1	15	1
No. 5, April 2	Cotyledons and first pair of leaves	1	15	12
	6 to 8 leaf stage	1	15	3
No. 6, July 14	5-months old	2	20	0
Season of 1921:				
No. 7, July 2	4 months old	2	10	1
	2 months old	2	11	2
No. 8, September 20	8 to 9 leaf stage	2	6	1
No. 9, October 14	10 to 16 leaf stage	2	14	1

OTHER PLANTS SUSCEPTIBLE TO CURLY-TOP

A list of plants found susceptible to curly-top has been previously given (*8*). Since that time no extensive effort has been made to determine what other plants may be affected by the disease. The annual (redmaids) *Calandrinia menziesii* T. and G., may now, however, be added to the list of those plants proved to be susceptible (Pl. 5, A and B.) This species is of special interest in this connection because it is one of the early winter annuals and probably serves along with (alfileria) *Erodium cicutarium* in harboring the curly-top virus over winter.

Among cultivated plants the tomato, *Lycopersicon esculentum* Mill, may now be included among the susceptible species. The effects of the disease on the tomato are rather of the mosaic type, a clearing of the veins of the younger leaves which gives these a slightly mottled appearance and a curling and distortion of the youngest leaves. Affected plants gradually wilt, turn yellow, and die within a few weeks after infection. The disease has not been found in commercial plantings, so far as is known to the writers. This is probably explained by the fact that the tomato seems to be unfavorable as a food plant for the leaf hopper. The variety known as Stone was used in the inoculation experiments.

The case of goose-foot, *Chenopodium murale*, is of special interest in considering the susceptibility of other plants. In the list previously published it was given as nonsusceptible. Before the time of that publication, nine experiments in regard to the susceptibility of *C. murale* had been performed. Viruliferous leafhoppers were caged on young plants in the attempt to produce the disease, or nymphs reared from viruliferous females on *C. murale* were tested on beets. The results of all these tests indicated that the species was not susceptible to the disease. The fact may be of some significance that all these early experiments were made at Spreckels, Calif., where the climate is usually cool. During the year 1919 and the two subsequent seasons, further tests were made at Riverside, Calif. In some instances the results were in part or entirely positive. In other words, *Eutettix tenella* nymphs reared on *C. murale* from viruliferous females produced curly-top in some or all of the plants to which they were transferred. Out of 43 experiments, however, only 13 gave positive results. The positive results show that under some conditions the plant harbors the virus of curly-top. In no case have clearly defined symptoms, such as swelling of the leaf veins or veinlet clearing, been noted, but in some of the plants a dwarfing of the later growth which may have been due to the disease has been observed. The fact that positive results were obtained in so small a proportion of the later tests and in none of

those done earlier shows that in its relation to this disease the species is peculiar. The climate of Riverside is in general warmer than that of Spreckels, particularly in summer, but opposed to the idea that climatic differences may explain the difference in results in the two localities is the fact that some of the positive results were secured during the winter. It seems probable that the species is resistant to curly-top.

An interesting observation made in connection with two of the experiments seems probably due to this seeming resistance. In two of the tests where nymphs from *Chenopodium murale*, the progeny of viruliferous leafhoppers, were caged on healthy young beets several of the beets soon developed faint clearing of the veins of some of the youngest leaves. The first symptom of curly-top is a clearing of the veins of the younger leaves. In these two tests, however, the vein clearing gradually disappeared in most of the plants and normal growth was continued. Only one or two plants developed typical cases of curly-top. One theory, which seems a plausible explanation, is that by passage through the *C. murale* the curly-top virus was so weakened or modified as to be rendered unable, in most cases, to effectively establish itself in the sugar beet. The point has not as yet been determined as to whether by means of nonviruliferous leafhoppers the virus may be obtained from those beet plants which show the faint vein clearing and subsequently recover.

As to variation in susceptibility to infection, the fact has been previously mentioned (*8*) that *Stellaria media* seems much more readily infected than the beet or buckwheat. There are some indications that *Erodium cicutarium* and *E. moschatum* and possibly *Calandrinia menziesii* are more readily infected than the beet. These three species, as well as spinach and tomato, die quickly as a result of the disease and in that sense are much more susceptible to the disease than several other species, e. g., *Malva parviflora*, cheese weed, and the sugar beet.

OVERWINTERING OF THE VIRUS

Few if any of those leafhoppers which leave the beet fields in the fall ever return. The observations by which this fact was established were in the main made in California. An observation made in Utah in the early summer of 1922 supports the belief that the same situation exists in that region. Near Elsinore, Utah, two sugar beet fields were inspected. In one of these fields a few cases of curly-top were found by diligent search, but certainly less than one-half of 1 per cent of the plants were affected. In the other field 1,200 plants were counted without finding any case of the disease. In both of these fields beet leafhoppers were present, and they had been there long enough to allow a considerable number of nymphs, their progeny, to emerge. It was estimated that there were 50 to 75 nymphs on each plant. Although the leafhoppers must have been on the beets for at least a month, there was practically no curly-top. Evidently most of the insects which flew into these fields in spring were nonviruliferous.

The question therefore arises as to where the new brood of insects which enters the fields in spring secures the curly-top virus. The suggestion has been previously made (*8*) that from susceptible annuals of the natural breeding areas some of these spring-brood leafhoppers may secure the virus. That this is not the only way in which the virus probably passes the winter should be made clear. As mentioned elsewhere in this paper, a small proportion of the leafhoppers usually remain in the cultivated area in the fall after the main body of the insects has departed. These "hold-over" insects, or "stragglers," being viruliferous, infect some of the early planted beets. Beets thus infected then serve as a source of virus for nonviruliferous insects that may come in later.

A third possible way in which the virus may be carried over winter is in old diseased plants growing in or near beet fields. In almost every old beet field such plants can be noted as making renewed growth in the spring. Frequently such plants are affected with curly-top. They would therefore serve as sources of the virus for any nonviruliferous insects that happened to feed on them.

CONTROL MEASURES

LEAFHOPPER CONTROL

The control of the beet leafhopper is naturally the first idea suggested for the prevention of curly-top damage, because this insect is the only known agency by which the disease is spread. The only feasible time of attack on the insects is in the early spring, when they first enter the beet fields and before they have deposited many eggs. They must then be killed or caught. The writers have tried the use of a hopperdozer. Large numbers of the insects were caught, but such a considerable proportion escaped that little or no benefit resulted. Liquid and dust sprays as insecticides and repellants have been tried to a limited extent by the writers. Kerosene emulsion in 6, 12, and 18 per cent strengths were tried. No significant decrease in the amount of curly-top resulted, even though some of the insects were killed. Nicotine sulphate in three different strengths gave only similar results. As repellants the following were tested: Bordeaux mixture, oil of citronella, naphthalene diluted with equal parts of lime, and mixtures of sulphur and tobacco dust with lime. In none of these tests was the benefit worthy of consideration. As has been mentioned before, the use of dusts, particularly mixtures containing nicotine sulphate, has been tried by others (*12*). The results thus far reported are not encouraging from the standpoint of commercial practice.

Control of the leafhopper by means of its natural enemies has been considered. There are three species of egg parasites and at least four parasites of the nymphs and adults. These parasites no doubt hold the leafhoppers in check to a large extent, but they can not be relied upon to prevent the production of curly-top in disastrous amounts.

TIME OF PLANTING

The control of *Eutettix tenella* by artificial means or by natural enemies seems at best a remote possibility, but by planting the beets early the damage due to this leafhopper can be avoided to a large extent. Emphasis should be placed in this connection on the fact that by early planting is not meant planting as early as possible in the fall, e. g., in October, but rather in the latter part of November and December, or as soon thereafter as practicable, and, for most of the affected regions, not later than February, if possible. Striking evidence in regard to the time-of-planting question was afforded by field observations in California in the season of 1918 at Corcoran and Bakersfield in the San Joaquin Valley and at Lancaster in the Mojave Desert. At Lancaster and Corcoran small plats of beets planted very early in the winter (October and November) were much more seriously diseased than were adjacent plats planted a month or two later. At Bakersfield, where the curly-top injury has usually been great, practically all of the planting of the season of 1917–18 was done in November, December, and January, and a good crop was produced, the beets being well advanced in size before the leafhoppers became abundant. At Corcoran, on the other hand, in the near vicinity of Lake Tulare, where the slow drying out of the soil retarded operations so that planting was delayed, as late as the latter part of March in some cases, great injury from curly-top resulted. In the vicinity

of Riverside and San Bernardino, in southern California, good crops have been produced by early planting (November and December), while the crops from late planting (March) in the same season were practically complete failures.

In regard to the time-of-planting question, from the standpoint of minimizing the injury from curly-top, two points must be given especial consideration. The plantings must not be made early enough in the fall to expose the young plants before the movement of the leafhoppers from the cultivated fields or late enough in the spring so that the beets will not have made a vigorous growth before the leafhoppers move into the cultivated areas. Mention should be made of the fact that usually some of the leafhoppers remain in the cultivated areas through the winter and that these stragglers may cause a considerable amount of damage. In general, however, the damage from those that remain in the cultivated areas, as compared with the damage when the main body of the insects is in cultivated districts, is relatively slight. With varying seasons the optimum time of planting will no doubt vary, but in general the safest plan is to plant as soon as possible after the middle of November and at least before the end of February. This recommendation is based primarily on conditions in California.

RESISTANT STRAINS

The fact that in almost every severely affected beet field a few individual plants will stand out conspicuously less affected than the rest has been noted by previous workers. The writers have repeatedly made this same observation. A project has been started by selecting the seemingly resistant plants from commercial fields, believing that by selection and possibly breeding a resistant strain satisfactory for commercial purposes may be developed.

Difficulties have been encountered in keeping over winter the beet roots which had to be removed from the field before harvest time. Siloing the beets in the ground, as is done in colder climates, has been found impracticable. Different methods of cold storage have been tried and a way of packing the roots for this purpose has been tested which seems, from the experience of one year, fairly satisfactory. Direct transplanting of the roots when harvested has been tried to a limited extent and found satisfactory.

Seed was produced from a few of the selected beets in the summer of 1921. Plantings of these strains together with control plats of commercial seed were tested for resistance in the autumn of that year. This test was made at Riverside, Calif., where leafhoppers were naturally abundant. In addition to the natural exposure, each plant of the selected strains was inoculated by caging on it a viruliferous leafhopper. The results of the test gave support to the belief that a strain of beets resistant to curly-top may be developed. Seeming differences in degree of resistance were noted between several of the selected strains and the commercial beets, and in one case this difference was marked (Pl. 5, C). Tests of these strains were made in the same manner but on a larger scale in the summer of 1922. The situation was complicated in this season by the fact that a large proportion of some of the apparently resistant strains developed seed stalks. On this account no satisfactory conclusions could be drawn as to resistance. Work is now in progress to determine the factors causing the premature seeding so that these factors may be eliminated.

More selections were made from commercial fields in California and Utah and also from the progeny test plats in the summer of 1922. The selection of more individuals from commercial fields and from the progeny plats will be continued and the progeny of these selections tested by inoculation for resistance to curly-top. The practice being followed in the growing of seed from the selected strains is to plant the mother beets singly or in small groups in private gardens, so that they will be isolated from each other.

SUMMARY

Curly-top disease of beets is characterized by a dwarfing of the whole plant, curling of the leaves, and irregular swelling of the veins on the under sides of the affected leaves. Marked phloem necrosis is produced throughout and shows as more or less conspicuous dark rings in cross sections of the root.

The disease is known to occur in only the semiarid regions of the western part of North America.

Curly-top is the cause of greater losses than any other sugar beet disease in this country. Very great damage to beets results when they are grown as an annual crop and when grown for seed production.

The exact nature of the cause of the disease is unknown, but the fact has been demonstrated that the virus can be transmitted by the beet leafhopper (*Eutettix tenella* Baker). No other means of transmission is known. The ability to produce the disease is not inherent in the leafhopper. There is some evidence that an interval of a few hours, an incubation period, must elapse after a nonviruliferous leafhopper has fed on a diseased plant before it can effectively transmit the virus to a healthy plant. Ten or more insects are more likely to produce the disease in an inoculated plant than when the inoculation is made with one or two insects. In cases where the disease is produced there is no difference in the incubation period or severity of the effect between inoculation with single insects and those with ten insects. A viruliferous leafhopper may not produce the disease each time it feeds on a healthy plant, even though the periods of feeding be 24 or 48 hours or even longer.

Tests in regard to the relation of light to infection indicate that plants kept in darkness during inoculation are more readily infected through the cotyledons than through the true leaves.

Tests of the effect of heat on the disease indicate that the virus is not destroyed by temperatures lower than those at which the beet tissue is killed.

Limited data suggest that the virus may be destroyed by desiccation.

The virus is distributed through all parts of an affected plant.

Limited data suggest evidence opposed to the claim that a specific bacterial organism is associated with curly-top.

The incubation period of the disease varies usually from 7 to 14 days. As short an incubation period as 4 days has occasionally been noted.

The incubation and development of the disease is retarded by low temperatures.

Very young plants are more readily infected than are older plants.

A wide range of species has been found susceptible to curly-top.

The virus probably overwinters in susceptible wild annuals, in volunteer beets, and in the insect.

No satisfactory control of the leafhopper by artificial or biological means has been discovered. Early planting usually avoids much of the injury. There is basis for belief that a resistant strain of beets may be developed.

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PLATE 1

Early stage of curly-top. Note the swelling of the veinlets on the lower surface of one leaf and the irregularity of the upper surfaces and the curled condition of the other young leaves.

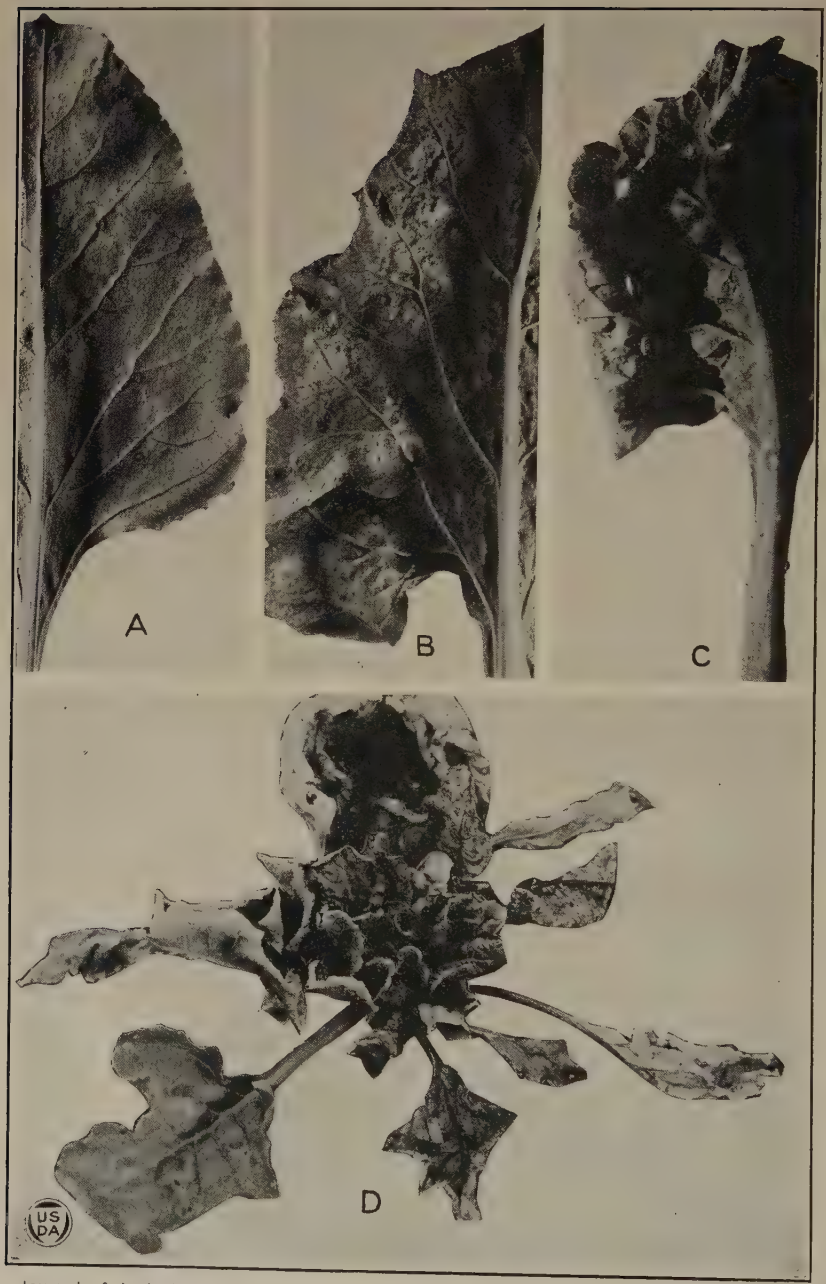
A
B
C
D
USDA

PLATE 2

A.—A type of curly-top beet leaf. Note the inconspicuous rounded swelling scattered over the surface.

B.—Curly-top beet leaf. Note the general distribution of the moderate, irregular swellings on the smaller veins. This specimen is representative of one type of response to the disease stimulus.

C.—Exudate on a curly-top leaf. The clear, viscid exudate has a sweet taste Fehling's test reveals the presence of sugars after hydrolysis with acid.

D.—Sugar beet curly-top. Plant inoculated on July 19, 1918, and photographed on August 29, 1918. Note the length of the old leaves, which were about mature when the plant was infected, in contrast with the dwarfed younger leaves.

PLATE 3

A.—Cross section of lateral vein of a healthy beet leaf.

B.—Cross section of lateral vein of a curly-top beet leaf. Note necrosis in the phloem region.

C.—Cross section of a young, curly-top beet root. Note the dark circle of necrotic phloem. All X about 70.

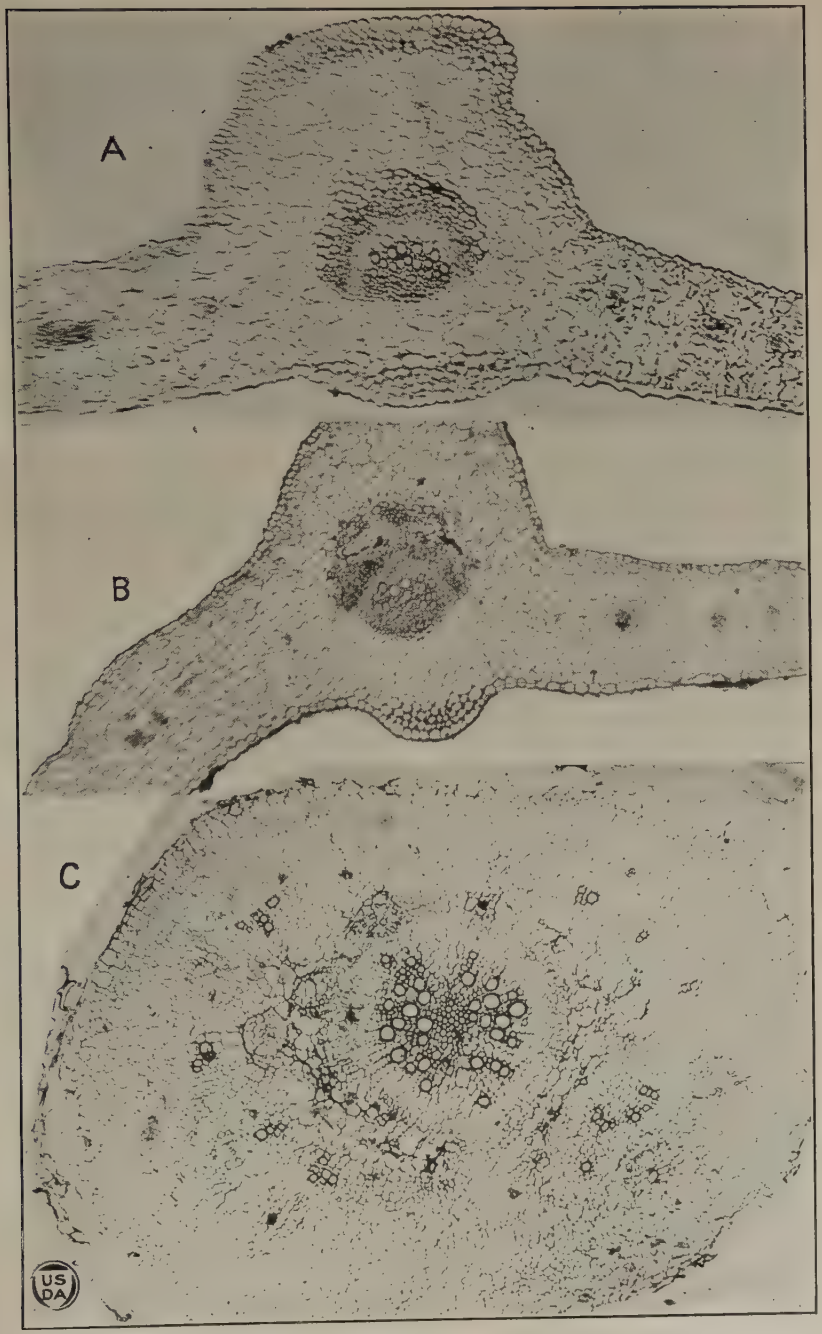
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PLATE 4

Sections of a curly-top beet root. The phloem necrosis which shows as the darkened tissues is often less conspicuous than in this specimen. X 2.

PLATE 5

A.—*Calandrinia menziesii* T. & C. Normal plant.

B.—Plant of about the same age but affected with curly-top. From plants diseased, as is *B*, from inoculation with viruliferous insects the disease has been communicated to healthy beets by the use of nonviruliferous leafhoppers.

C.—Resistance to curly-top. The beets in the row on the right were the progeny of a plant selected for resistance. The control row adjacent on the left was from commercial seed. Both rows were exposed to the same natural infestation of leafhoppers, and in addition all the plants of the selected strain had viruliferous leafhoppers caged on them.

B
A
C
USDA